FLIGHT SPEEDS OF NORTHERN PINTAILS DURING MIGRATION DETERMINED USING SATELLITE TELEMETRY

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ABSTRACT.—Speed (km/hr) during flight is one of several factors determining the rate of migration (km/ day) and flight range of birds. We attached 26-g, back-mounted satellite-received radio tags (platform transmitting terminals; PTTs) to adult female Northern Pintails (*Anas acuta*) during (1) midwinter 2000–2003 in the northern Central Valley of California, (2) fall and winter 2002–2003 in the Playa Lakes Region and Gulf Coast of Texas, and (3) early fall 2002–2003 in south-central New Mexico. We tracked tagged birds after release and, in several instances, obtained multiple locations during single migratory flights (flight paths). We used data from 17 PTT-tagged hens along 21 migratory flight paths to estimate groundspeeds during spring (n = 19 flights) and fall (n = 2 flights). Pintails migrated at an average groundspeed of 77 ± 4 (SE) km/hr (range for individual flight paths = 40–122 km/hr), which was within the range of estimates reported in the literature for migratory and local flights of waterfowl (42–116 km/hr); further, groundspeed averaged 53 ± 6 km/hr in headwinds and 82 ± 4 km/hr in tailwinds. At a typical, but hypothetical, flight altitude of 1,460 m (850 millibars standard pressure), 17 of the 21 flight paths occurred in tailwinds with an average airspeed of 55 ± 4 km/hr, and 4 occurred in headwinds with an average airspeed of 71 ± 4 km/hr. These adjustments in airspeed and groundspeed in response to wind suggest that pintails migrated at airspeeds that on average maximized range and conserved energy, and fell within the range of expectations based on aerodynamic and energetic theory. *Received 19 November 2004, accepted 6 September 2005.*

The overall rate at which birds travel during migration, often referred to as migration speed (measured in km/day), includes the time required to accumulate fat reserves and rest prior to migration and at stopovers, and the actual time spent in flight during which fat is catabolized (Alerstam and Lindström 1990). Flight speed (km/hr) is expressed as groundspeed (velocity with respect to ground) or airspeed (velocity with respect to air); the ratio of groundspeed to airspeed directly measures the effects of wind on the energetic costs of migration (Alerstam 1978, Richardson 1990). This ratio is proportional to migration speed (Alerstam 2003), and can predict the strength of migration (the number of birds aloft; Richardson 1990). For many birds, migration speed may be controlled largely by the time required to acquire fat reserves at stopovers (Alerstam 2003). However, Liechti and Bruderer (1998) concluded that for birds making long nonstop flights, selection of favorable tailwinds to boost groundspeed and save energy (fat) is more important than timing departure based on the rate of fat accumulation. Birds in headwinds, for example, may lower flight altitude until wind velocity declines, thereby increasing groundspeed and conserving energy (Kerlinger and Moore 1989).

Birds migrate at groundspeeds that reflect, among other things, airspeed in the presence or absence of tailwinds or headwinds (Richardson 1990, Alerstam 2003) and aerodynamic characteristics of the species (Pennycuick 1975, Rayner 1990). Aeronautical flight mechanics and bioenergetics theory suggest that birds should fly at one of two characteristic airspeeds during migration. The first minimizes energy cost per unit of time to remain airborne as long as possible (minimum power speed; V_{mp}), and the second minimizes the energy cost per unit of distance flown to maximize distance over the ground with a certain fuel load (maximum range speed; V_{mr}) (Tucker

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and Schmidt-Koenig 1971, Alerstam and Hedenström 1998). A third conceptual speed, which is not as well defined (Bruderer and Boldt 2001), minimizes total duration of the migration by maximizing overall speed (minimum time speed; V_{mt}); however, in practice it is rarely separable from V_{mr} (Alerstam and Hedenström 1998, Hedenström and Alerstam 1998). In general, waterfowl are well designed for relatively rapid long-distance migration (Rayner 1988), and the moderately sized Northern Pintail (*Anas acuta*), in particular, features an aerodynamic design (streamlined shape, long narrow wings) that supports efficient long-distance flight (Pennycuick 1975, Bellrose 1980, Bruderer and Boldt 2001). However, it is not known whether pintails migrate with flight speeds that adhere to theoretical models.

Investigators have used satellite telemetry to estimate the groundspeeds of migrating swans (*Cygnus* spp.; Pennycuick et al. 1996a, Ely et al. 1997) and Brant (*Branta bernicla*; Green et al. 2002), but we found no such information for ducks. A recent project to track migration of adult female pintails outfitted with satellite-receiving radio tags (platform transmitting terminals; PTTs) in California, Texas, and New Mexico wintering regions (Miller et al. 2001, 2005) provided an opportunity to directly estimate groundspeed. By using archived speeds and directions of winds at a typical waterfowl migration altitude, we then determined their potential airspeed and compared it with theoretical values of V_{mp} and V_{mr} (Bruderer and Boldt 2001).

METHODS

We captured pintails at the following times and locations: (1) December–January 2000–2003 in California at Sacramento Valley national wildlife refuges (NWR) and state wildlife areas (central location: 39° 24′ N, 121° 58′ W); (2) November–January 2001–2002 in the Playa Lakes Region of Texas at Buffalo Lake NWR (34° 54′ N, 102° 7′ W) and on private lands (33° 46′ N, 101° 51′ W), and along the Texas Gulf Coast on a unit of Aransas NWR (28° 33′ N, 96° 33′ W) and on private lands (27° 20′ N, 97° 48′ W); and (3) October–November 2001–2002 in New Mexico at Bosque del Apache NWR (33° 48′ N, 106°

51′ W). These areas are located in important pintail wintering or fall staging regions (Bellrose 1980).

We tagged only adult female pintails because of their critical role in population dynamics (Flint et al. 1998). We sorted all hens by sex and age (Carney 1992), attached federal leg bands, and obtained body mass (±5 g). We used Model 100 PTTs from Microwave Telemetry, Inc. (Columbia, Maryland), and annually attached 25–55 on females in California, 20 in Texas, and 6–9 in New Mexico. The units, with harness and protective neoprene pad, weighed about 26 g, which was 2.7–3.2% of average body mass at capture in California (900–950 g), Texas (820–920 g), and New Mexico (935–975 g), well under commonly used guidelines (Caccamise and Hedin 1985). We attached each PTT dorsally between the wings by fashioning a harness of 0.38-cm-wide (sold as 3/16 in) Teflon ribbon (Bally Ribbon, Bally, Pennsylvania). The completed harness included fore and aft body loops connected with a 1-cm-length of ribbon over the keel, similar to designs used by Malecki et al. (2001). Ours, however, consisted of a single length of ribbon without metal clips, buckles, shrink-tubing, or sewed areas, and we hardened knots with cyanoacrylate glue. We released tagged hens at trap sites 5–19 hr after capture—either during evening pintail flights or at night.

To encompass spring migration, we programmed PTTs to last 6–8 months by using a repeating duty cycle consisting of a 5- to 6-hr transmission period followed by a 72-hr resting period; some PTTs lasted long enough to provide data during fall migration. We used the Argos location and data collection system (Argos, Inc. 1996), including multi-satellite service with standard and auxiliary location processing, to monitor the locations of PTT-tagged pintails. Argos estimates PTT locations from the Doppler shift in transmission frequency received by satellites as they approach and then move away from the PTT. Argos checks the plausibility of locations via (1) minimum residual error, (2) transmission frequency continuity, (3) shortest distance covered since previous location, and (4) plausibility of velocity between locations. The number of positive checks (NOPC; 0–4) is included with each location received via daily

e-mails. The PTTs also provided sensor data to index the unit's temperature, remaining voltage, and motion. We used these, especially the latter, to determine whether birds were alive and to verify that they were flying.

Argos classifies each PTT location based on estimated accuracy and the number of transmissions (messages) received from each PTT during a satellite overpass. The classes of location quality (LC 3, LC 2, LC 1, LC 0) are based on ≥4 messages received by the satellite via standard data processing; respective accuracies are <150, 150–350, 350–1,000, and >1,000 m. Accuracy is expressed as the probability that 67% of the locations will fall within stated limits; therefore, high-quality locations might be inaccurate, while lower-quality locations might be very accurate (Hatch et al. 2000). Argos does not estimate accuracy of LC A (3 messages received), LC B (two messages received), or LC Z (latitude/longitude often provided if ≥1 message received), which are received via auxiliary processing; however, field tests have shown that LC A can be as accurate as LC 0 or LC 1 (Britten et al. 1999, Hays et al. 2001), and LC B can be as accurate or better than LC 0 (Hatch et al. 2000, Hays et al. 2001). Therefore, the accuracy of individual points along a flight path likely varies, even among those of the same LC (Hatch et al. 2000). If a PTT-tagged bird is stationary (not flying), several criteria are normally used to choose one best location from among the many normally provided by Argos (Ely et al. 1997, Butler et al. 1998, Petersen et al. 1999, Hatch et al. 2000). Because of continuous forward travel, however, Argos cannot provide alternate points at each location for pintails in migratory flight. Therefore, we initially plotted all locations of birds in flight and subsequently examined each of them in detail to determine flight paths.

We analyzed and displayed location data using ArcInfo and ArcView Geographic Information System software (Environmental Systems Research Institute, Redlands, California). For each female, we plotted individual flight paths using all PTT locations acquired while the bird was flying. Each flight path consisted of segments formed by successive pairs of adjacent location points (e.g., a path formed by five points would have four flight-path segments). We used only locations recorded during pintail migratory flights—identified from multiple locations of birds heading generally northerly or southerly during a single transmission period—concurrently with PTT motion sensor data that suggested vigorous activity. Additionally, we used only locations >200 km from the location recorded on the previous or subsequent (or both) location-days; these criteria precluded inadvertently including stationary pintails or those making only local flights.

We selected only those points that best defined the flight path, and deleted those that deviated from the general line of flight, reversed direction, occurred in clusters (indicating a stationary bird), occurred too close together in space and time, or represented movement too fast or too slow between points—especially if LC was A or worse (Hatch et al. 2000 used LC 0). For example, we considered a given point to be an obvious outlier from the general line of flight if the perpendicular distance from the flight line was greater than the average error distance from true position as determined for the least accurate LCs in recent field tests of PTTs (i.e., 7.5 km for LC 0 and LC A, and 23–35 km for LC B [Blouin et al. 1999, Britten et al. 1999]; 20 km for LC A and LC B [Hatch et al. 2000]; 1–10 km for LC 0 and LC A, and 7 km for LC B [Hays et al. 2001]). We also considered points to be outliers if the time between location points along the path was <10 min and the distances between them <20 km, unless this was typical along the flight path and produced similar intervening groundspeeds among segments. We rejected one of two points that created sharp-angled direction changes (usually >45°) and reversals. Additionally, we questioned the accuracy of individual locations if the groundspeed along path segments seemed biologically impossible. We defined this as (1) >160 km/hr, the speed of a Red-breasted Merganser (*Mergus serrator*) flying with a 32 km/hr tailwind, while being chased by a small aircraft (Thompson 1961), or (2) <20 km/hr when point separation was <20 km, unless intervening groundspeeds matched those between other more widely separated points along the path. These criteria are somewhat arbitrary, but provided a consistent method for selecting and rejecting locations—similar to procedures used by Hatch

et al. (2000), in which they discarded locations "conspicuously outside" clusters of points (stationary birds) because they violated their redundancy rule.

We estimated apparent groundspeeds along each outlier-corrected flight path by summing the total time (hr) and distance (km) of each flight-path segment, and then dividing total distance over the flight path by total time from the first to the last accepted location point. We used multiple flight paths from individual tagged hens, if available, and estimated groundspeed as mean ± SE for all flights. For comparison, we also estimated groundspeed for all flights using all recorded locations (outliers retained) to recognize our uncertainty with the deletions and determine how our criteria may have affected final groundspeed estimates.

We wanted to determine reliable airspeeds for PTT-tagged pintails, but wind speeds increase and their directions change markedly with increasing altitude (Kerlinger and Moore 1989, Ahrens 2000); in addition, we did not know at what altitudes our tagged ducks migrated (our PTTs did not have altitude sensors). We had no means to predict when or where measurable flight paths would occur, and as a result, we could not *a priori* deploy radar and weather balloons to obtain groundspeed, wind speed, wind direction, and flight altitude simultaneously, as done when birds pass predictable locations (Bruderer and Boldt 2001). Therefore, to assess the effect of headwinds or tailwinds along the 21 pintail flight paths, we assumed migration altitudes of sea level and 1,460 m above sea level (1,000 and 850 millibars [mb] at standard pressure; Ahrens 2000), which is within the typical range used by migrating waterfowl (Kerlinger and Moore 1989, Berthold 1996), and for which archived weather data were readily available. The higher altitude was used by Dau (1992), Shamoun-Baranes et al. (2003), and Gill et al. (2005) to examine migration of Brant, White Storks (*Ciconia ciconia*), and Bar-tailed Godwits (*Limosa lapponica*), respectively. We obtained wind speed and direction on the dates of pintail flights using North American Constant Pressure weather charts (850 mb) for 00:00 UTC and 12:00 UTC, published by the National Center for Environmental Prediction (NCEP; National Climatic Data Center 2005).

We assumed that the weather charts represented conditions at the location of flying pintails, and we used wind speeds and directions nearest to each pintail flight path (Shamoun-Baranes et al. 2003). Because exact flight altitudes remained unknown, we did not add unjustified precision to the generally imperfect data to account for the angle at which tailwinds or headwinds may have intercepted pintail flight paths (Gill et al. 2005). Instead, we assumed that tailwinds and headwinds essentially paralleled flight paths, and ignored compensation and drift (Wege and Raveling 1984, Alerstam and Hedenström 1998). We calculated airspeeds either as (1) groundspeed − tailwind or (2) groundspeed + headwind. To characterize migration conditions at the surface, we obtained archived sky conditions and surface wind speed and direction at the time of flights from weather stations nearest the flight paths (Weather Underground 2005).

RESULTS

During 2001, 2002, and 2003, we obtained 21 flight paths of 17 PTT-tagged pintails for which we estimated groundspeeds (Fig. 1). Of this total, 19 flights from 16 pintails occurred during spring, and 2 flights from 2 birds occurred during fall (1 hen provided 1 spring and 1 fall flight; Table 1). These data included 14 pintails tagged in California, 2 in Texas, and 1 in New Mexico. We used all original Argos locations from 10 pintail flight paths (uncorrected), but deleted ≥1 location from each of 11 others (outlier-corrected), because they did not meet our established criteria. Outlier correction resulted in increases in groundspeed of 4–21 km/hr for five flight paths, decreases in speed of 1–69 km/hr for five flight paths, and no change for one flight path. Outlier correction reduced our total number of locations from 108 to 77. Correction for outliers did not markedly increase the proportion of high-quality locations forming flight paths compared with that in the uncorrected data set. For example, the proportion of LC 1 and LC 2 locations increased to 17% from 12% of all locations, and those of LC A, B, and Z declined to 25% from 32% (no change in proportion of LC 0).

When we used the 11 outlier-corrected flights and the 10 uncorrected flights, groundspeeds of pintails along all 21 flight paths
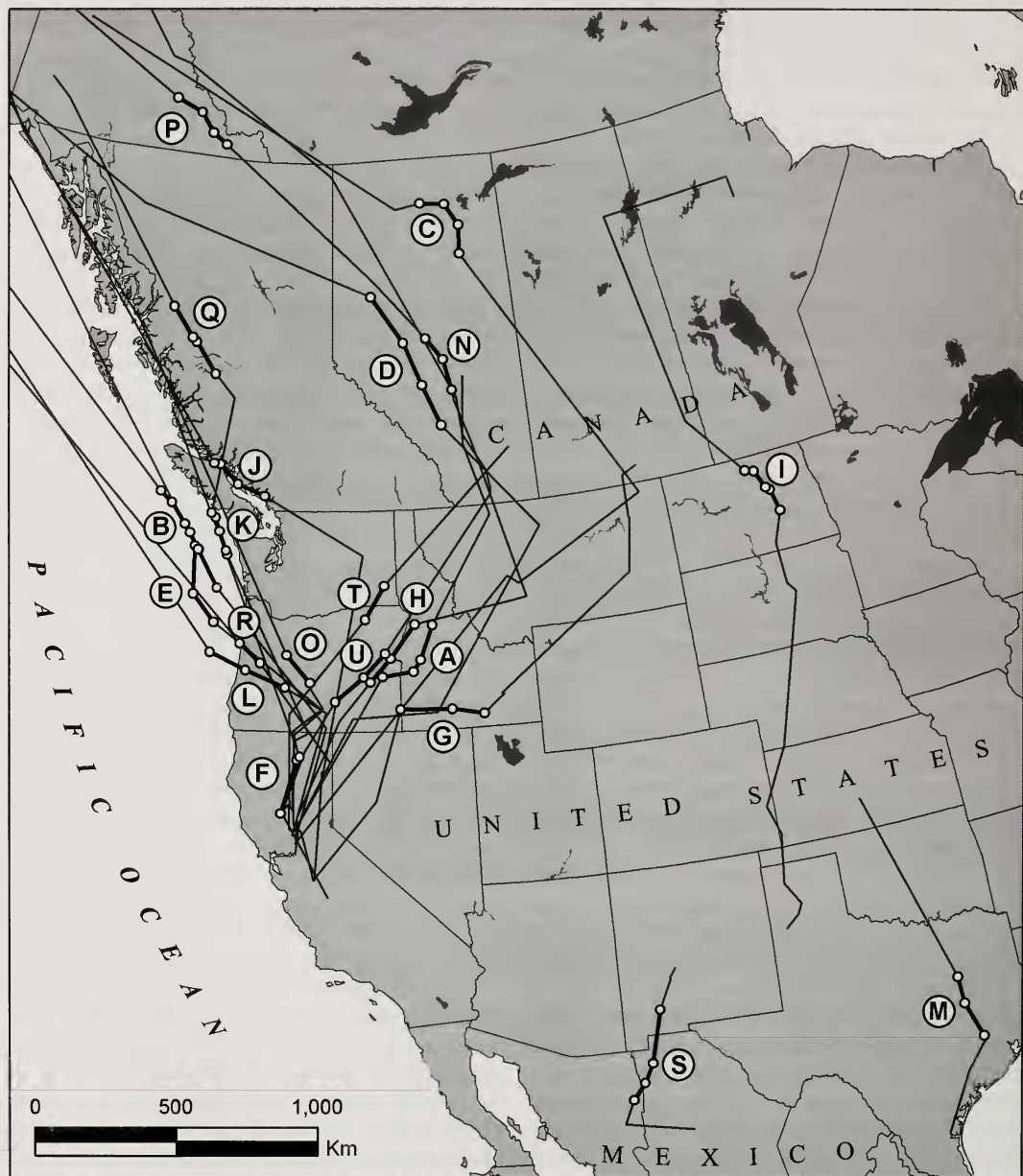
FIG. 1.   Migration flight paths and path segments of adult female Northern Pintails PTT-tagged in California, Texas, and New Mexico, used to estimate groundspeed and airspeed (km/hr), 2001–2003. Circled uppercase letters are bird identifiers from Tables 1, 2. Thick black lines show the measured flight paths divided into segments by open circles representing pintail locations. Thin gray lines show migration routes prior and subsequent to the measured path.

ranged from 40 to 122 km/hr (Table 1) and averaged 77 ± 4 km/hr (CV = 5.6, 90% CI = 69–84). Two-thirds of the speeds (14 of 21 flight paths) occurred over a narrower range of 61–80 km/hr. Without omitting outliers, groundspeeds ranged from 45 to 111 km/hr and averaged 78 ± 4 km/hr (CV = 4.9, CI = 72–84), indistinguishable from the outlier-corrected value. Groundspeed averaged 75 ± 4 km/hr (CV = 4.6, CI = 70–81) for the 10

TABLE 1. Outlier-corrected groundspeeds of adult female Northern Pintails, including start and end times, distance flown, and time in flight, along flight paths determined via satellite telemetry, 2001–2003. All times are Pacific Standard Time, except as noted. Bird identifiers (uppercase letters) correspond to those in Figure 1.

Year	Start date	Bird	Location of flight (n_1, n_2)[a]	Start-end times	Distance flown (km)	Time in flight (hr)	Ground speed (km/hr)
2001	21 Mar	A	West-central Idaho (4, 4)	04:15–08:42[e]	288.7	4.45	65
2001	25 Apr	B	West of Washington/British Columbia (8, 6)	03:55–09:23	393.3	5.45	72
2001	27 Apr	C	Northeastern Alberta (10, 5)	04:29–07:58[e]	267.4	3.49	77
2001	27 Apr	D	Western Alberta (4, 4)	19:31–00:38[e]	511.4	5.12	100
2001	3 May	E	West of Washington/Oregon (4, 4)	02:30–06:23	309.2	3.90	79
2002	23 Feb	F	Northern California (8, 3)	17:05–20:06	212.6	3.13	68
2002	20 Mar	G	Southern Idaho (4, 3)	01:09–03:42[e]	294.4	2.55	116
2002	21 Mar	H[b]	Eastern Oregon to western Idaho (3, 3)	19:55–23:57[e]	257.8	4.03	64
2002	13 Apr	I	North Dakota (10, 5)	15:54–19:52[f]	180.1	2.28	79
2002	19 Apr	J	British Columbia coast (7, 4)	02:20–07:13	216.3	4.89	44
2002	21 Apr	K[c]	West of Washington/British Columbia (8, 5)	11:51–15:46	157.6	3.91	40
2002	24 Apr	L[d]	Western Oregon/ocean (3, 3)	23:17–01:25	292.7	3.79	77
2002	25 Apr	M	Eastern Texas (3, 3)	20:41–22:20[f]	218.3	3.06	71
2002	8 May	N[b]	Central Alberta (3, 3)	21:08–22:49[e]	206.1	3.36	62
2002	9 May	O	Central Oregon (2, 2)	21:35–23:14	127.4	1.66	77
2002	14 May	P[b]	Southeastern Yukon (9, 5)	09:08–10:48	366.4	3.01	122
2002	26 May	Q[c]	West-central British Columbia (4, 3)	22:47–02:15	277.3	3.46	80
2002	10 Oct	R[d]	Western Oregon/ocean (3, 2)	21:38–23:16	99.8	1.64	61
2002	12 Nov	S	Southern New Mexico to Mexico (6, 5)	18:49–22:17[e]	428.1	4.51	95
2003	19 Mar	T	Northeastern Oregon (2, 2)	01:07–02:46	135.3	1.66	82
2003	31 Mar	U	Eastern Oregon (3, 3)	19:28–22:39	243.1	3.19	76

[a] n_1 = total number of separate location points recorded during flight and used to estimate groundspeed without correcting for outliers; n_2 = number of accepted location points used to estimate outlier-corrected groundspeed.

[b,c,d] Superscripts of the same letter indicate multiple flights for the same pintail.

[e] Mountain Standard Time.

[f] Central Standard Time.

uncorrected flights, 78 ± 8 km/hr (CV = 10.1, CI = 65–90) for the 11 outlier-corrected flights, and 80 ± 7 km/hr (CV = 8.4, CI = 69–91) for the 11 flights when not corrected for outliers. Most (19 of 21) flights occurred partially or entirely at night (Table 1), and two paths transited land and sea (Fig. 1).

Based on wind speeds and directions at 1,400 m (850 mb), 17 of the 21 flights (81%) occurred in tailwinds and four in headwinds (Table 2). Groundspeeds averaged 82 ± 4 km/hr (CV = 8.2, CI = 75–89) in tailwinds and 53 ± 6 km/hr (CV = 11.8, CI = 43–63) in headwinds. Three of the four flights that occurred in headwinds at 850 mb (birds A, J, and K; Table 2) would have had tailwinds near the ground surface of 6–13, 7–11, and 13–15 km/hr, respectively (weather station data), and the fourth flight (bird N) would have had headwinds of 6–9 km/hr. Corresponding airspeeds of pintails at 850 mb ranged from 24 to 97 km/hr in tailwinds and from 59 to 80 km/hr in headwinds (Table 2), with means of 55 ± 4 km/hr (CV = 7.9, CI = 48–62) in tailwinds and 71 ± 4 km/hr (CV = 6.2, CI = 64–78) in headwinds. The ratios of groundspeed to airspeed averaged 0.73 ± 0.6 in headwind (CV = 8.2, CI = 0.63–0.83) and 1.61 ± 0.14 in tailwind (CV = 8.5, CI = 1.39–1.83).

The longest distance flown by a pintail for which we estimated groundspeed (bird B), was 2,926 km—from Goose Lake in southern Oregon (42° 15′ N, 120° 23′ W) to the Kenai Peninsula in Alaska (59° 12′ N, 151° 46′ W; Table 1). Assuming that pintails flew at the

TABLE 2.   Airspeeds of adult female Northern Pintails estimated using satellite telemetry and supporting wind speed and direction data from North American Constant Pressure weather charts (850 millibars or 1,460 m), 2001–2003. Local sky and surface wind direction categories at weather stations nearest to flight paths are also given. Bird identifiers (uppercase letters) correspond to those in Figure 1.

Year	Date	Bird	Ground-speed (km/hr)[a]	Highest wind speed (km/hr)[b]	Wind direction (compass)[b]	Wind category[c]	Airspeed (km/hr)[d]	Local sky conditions; surface wind category[e]
2001	21 Mar	A	65	9	NW	QHW	74	MC; QTW[1]
2001	25 Apr	B	72	37	SSW	QTW	35	OC; QHW[2]
2001	27 Apr	C	77	19	SSW	QTW	58	OC; QTW[3]
2001	27 Apr	D	100	28	SSW	QTW	72	MC; none[4]
2001	3 May	E	79	46	SSW	QTW	33	PC; QTW[2]
2002	23 Feb	F	68	19	SSE	TW	49	OC; VAR[5]
2002	20 Mar	G	116	19	W	TW	97	CL; QTW[6]
2002	21 Mar	H[f]	64	28	SW	QTW	36	CL; QHW[7]
2002	13 Apr	I	79	28	SW	QTW	51	PC; TW[8]
2002	19 Apr	J	44	28	WNW	QHW	72	MC; QTW[9]
2002	21 Apr	K[g]	40	19	NNW, N	HW	59	LR; QTW[10]
2002	24 Apr	L[h]	77	19	SW	QTW	58	CL; VAR[11]
2002	25 Apr	M	71	28	WSW, SW	QTW	43	MC; QHW[12]
2002	8 May	N[f]	61	19	N	HW	80	OC; HW[4]
2002	9 May	O	77	9	SE	TW	68	OC; HW[13]
2002	14 May	P[f]	122	56	SE	TW	66	LR; QTW[14]
2002	26 May	Q[g]	80	56	SSE	TW	24	LR; QTW[15]
2002	10 Oct	R[h]	61	9	NW, NNW	TW	52	OC; none[11]
2002	12 Nov	S	95	28	NNW, N	QTW	67	CL; QTW[16]
2003	19 Mar	T	82	19	SSW	TW	63	CL; QTW[17]
2003	31 Mar	U	76	9	SW	QTW	67	R; QTW[18]

[a] Values rounded to nearest km/hr from Table 1.

[b] Wind speeds and compass directions obtained from airspeed/direction symbols on 850 mb constant pressure weather charts nearest pintail flights.

[c] Symbols for relative wind direction category apply to upper air and surface data: Q = quartering, TW = tailwind, HW = headwind, SW = sidewind, VAR = variable, none = calm.

[d] Airspeed = groundspeed – tailwind, or groundspeed + headwind; wind speed used is the highest of the ranges obtained from weather charts.

[e] Sky conditions: OC = overcast, LR = light rain, R = rain, MC = mostly cloudy, PC = partly cloudy, CL = clear; where >1 condition applied, we show the condition least favorable for migration. Numbered superscripts refer to the nearest weather station: 1 = Boise, Idaho; 2 = Hoquiam, Washington; 3 = Fort Smith, Northwest Territories; 4 = Edmonton, Alberta; 5 = Redding, California; 6 = Burley, Idaho; 7 = Ontario, Oregon; 8 = Jamestown, North Dakota; 9 = Vancouver, British Columbia; 10 = Quillayute, Washington; 11 = Newport, Oregon; 12 = College Station, Texas; 13 = Redmond, Oregon; 14 = Watson Lake, Yukon; 15 = Terrace, British Columbia; 16 = Truth or Consequences, New Mexico; 17 = Hermiston, Oregon; 18 = Burns, Oregon.

[f,g,h] Superscripts of the same letter indicate multiple flights for the same pintail.

average outlier-corrected groundspeed of 77 km/hr, they would have required 38 hr to complete the flight nonstop.

DISCUSSION

The estimated 77 km/hr migration groundspeed of PTT-tagged adult female pintails was consistent with that of the upper range of pintail groundspeeds (local flights) estimated using radar (65–76 km/hr; Bruderer and Boldt 2001). Average groundspeeds of other ducks during local flights have ranged from 42 to 116 km/hr (Speirs 1945, Lokemoen 1967, Kerlinger 1995, Bruderer and Boldt 2001), very similar to the range we obtained for migrating pintails. During migration, PTT-tagged Whooper (*Cygnus cygnus*) and Tundra (*C. columbianus*) swans migrated at 60–90 km/hr (Pennycuick et al. 1996a, Ely et al. 1997), and

Canada Geese (*Branta canadensis*) fitted with VHF radio-transmitters migrated at groundspeeds of 49–110 km/hr (Wege and Raveling 1984). Bellrose and Crompton (1981) clocked migrating Canada Geese at 61–73 km/hr, Lesser Snow Geese (*Chen caerulescens*) at 67–83 km/hr, and Mallards (*Anas platyrhynchos*) at 72 km/hr by following in automobiles or aircraft. Using satellite telemetry, radar, and other means, migrating Brant have been recorded at groundspeeds of 99 km/hr (Dau 1992), 90 km/hr (Lindell 1977 cited in Ebbinge and Spaans 1995), 30–115 km/hr (Green and Alerstam 2000), and 58–109 km/hr (Green et al. 2002). Wide interspecific variation in these reported groundspeed estimates probably resulted from species-specific flight aerodynamics (Pennycuick 1975, Rayner 1990), atmospheric conditions (Kerlinger and

Moore 1989), and errors associated with the various methods (Bruderer and Boldt 2001). The relatively wide range of pintail groundspeeds in our study undoubtedly reflected primarily wind conditions, and perhaps angle of flight (ascending, descending, horizontal; Green and Alerstam 2000); however, the close agreement between outlier-corrected and uncorrected data suggests that measurement error was minimal. We recommend that investigators report groundspeeds and groundspeed to airspeed ratios because of their implication in analysis of flight range and cost.

Birds use tailwinds to minimize the energetic cost of migration by increasing groundspeed and range, reducing airspeed to maintain groundspeed, or both (Richardson 1990, Alerstam and Hedenström 1998), and this has been verified for migrating waterfowl (Blokpoel 1974, Bellrose and Crompton 1981, Wege and Raveling 1984, Dau 1992, Green et al. 2002). Most pintails (had they migrated at our specified altitude of 1,460 m) would have benefited from tailwinds, as exemplified by their average higher groundspeed and lower airspeed in tailwinds. Birds are known to alter flight altitudes and move to those with favorable winds (Gauthreaux 1991). If three of the four pintails in our study that we assumed were flying into headwinds aloft had instead been flying near the ground surface, they would have had tailwinds. Also, the three flights occurred partially or completely during the day (Table 1), when low-altitude migration flights are typical (Richardson 1990). However, we cannot be sure of the migration altitude, and sky conditions observed from the ground varied from mostly cloudy to light rain and overcast (Table 2), weather types that tend to discourage migration (Richardson 1990).

Birds generally adjust airspeed when wind direction changes; waterfowl increase airspeed to compensate for headwinds and reduce airspeed as tailwinds increase (Tucker and Schmidt-Koenig 1971, Bellrose and Crompton 1981, Wege and Raveling 1984, Pennycuick et al. 1996a), but the adjustments are not necessarily proportionate (Bellrose and Crompton 1981). Our pintails clearly did not have a strategy to maintain airspeeds in changing wind conditions (Table 2), although Blokpoel (1974) concluded that migrating Lesser Snow Geese did. Our estimates of average pintail airspeed support the hypothesis that their airspeed was faster, and groundspeed slower, in headwinds compared with tailwinds. The ratios of groundspeed to airspeed for tagged pintails show that compared with still air (ratio = 1.0), pintails decreased their groundspeeds about 27% in headwinds and increased groundspeeds by about 61% in tailwinds, suggesting that migration occurred at V_{mr}. Demonstrating such compensation during local flights, Tucker and Schmidt-Koenig (1971) reported a pintail airspeed of 56 ± 1 km/hr with tailwinds and 66 ± 1 km/hr against headwinds, similar to our results (55 and 71 km/hr, respectively). Because Tucker and Schmidt-Koenig (1971) did not report respective groundspeeds or wind directions, we estimated groundspeeds from their study by using their reported average wind speeds of 18 and 31 km/hr and applying them as tailwinds and headwinds. This produced potential respective groundspeeds of 74 and 87 km/hr in tailwinds and 48 and 35 km/hr in headwinds, similar to our findings.

Using the theoretical flight models of Pennycuick (1989) and Rayner (1990), Bruderer and Boldt (2001) calculated V_{mr} and V_{mp} for pintails as 64 and 40 km/hr, respectively. The average airspeed of our pintails in tailwinds (55 km/hr) was above V_{mp} and below V_{mr}, and their average airspeed in headwinds (71 km/hr) was greater than both V_{mp} and V_{mr}. In four instances, our pintails flew more slowly than V_{mp} in tailwinds (24–36 km/hr), and on nine flight paths in variable wind directions, they flew faster than V_{mr} (66–97 km/hr); on eight paths, pintails flew at speeds between the theoretical speeds (43–63 km/hr; Table 2). Our data support Welham's (1994) findings that pintail-sized birds tend to migrate at V_{mr}, but are not bound by theoretical flight models (Pennycuick 1998); more data are needed to compare field results with their predictions. The four excessively slow speeds in tailwinds ($<V_{mp}$) may reflect errors resulting from overestimation of wind speed (Tucker and Schmidt-Koenig 1971), resulting from potential differences between winds at the actual (unknown) and selected (850 mb) flight altitudes. Pintails probably do not fly at the theoretical minimum power speed in any event, a phenomenon demonstrated for a Common Teal (*Anas crecca crecca*) and other birds that

refused to fly in wind tunnels at V_{mp} (Penny-cuick et al. 1996b). To address this problem in future field studies, wind speeds and directions will need to be obtained very near flight altitudes because wind data gleaned from constant pressure charts are only as relevant as the selected flight altitude. Investigators could use PTTs with onboard altitude sensors, but these sensors are not yet available for the small PTTs required for use on pintail-sized birds. Larger PTTs with GPS technology are available, which would be suitable for geese and swans; these can track position, altitude, heading, and speed with high accuracy (±30 m; Microwave Telemetry, Inc. 2005).

Most waterfowl are known to migrate at night as well as during daylight hours (Bellrose 1980, Kerlinger and Moore 1989). Therefore, it is not surprising that nearly all of our measured flights of tagged pintails occurred partially or entirely at night. For long-distance migrations, typically beginning after sunset (Kerlinger and Moore 1989), travel may extend into daylight hours because there is not enough time to make the transit during nighttime hours (Berthold 1996), or wind conditions might favor continuing into daytime hours (Liechti and Schaller 1999 cited in Jenni and Schaub 2003); five of our recorded flights overlapped day and night (birds A, B, C, E, and J; Table 1). Migration in the cooler, ambient nighttime air at moderate to high altitudes theoretically provides bioenergetic benefits of heat dissipation and water conservation through evaporative cooling (Berthold 1996, Kvist et al. 1998). This could be critical for waterfowl during long, nonstop migrations when diurnal and surface temperatures are high (e.g., early fall, late spring). Nocturnal atmospheric conditions provide distinct advantages to migrating birds, including cooler temperatures and more humidity, denser air, weaker and more laminar horizontal winds, and little or no vertical air motion compared with daytime conditions (Kerlinger and Moore 1989, Ahrens 2000); these conditions maximize flight speed while reducing energy cost. Additionally, night migration would enable celestial navigation (Bellrose 1980).

Our data suggest that researchers need not delete any but the most obvious outliers to estimate groundspeeds when using the method of total distance divided by total time with relatively large sample sizes. Average groundspeed estimated using all data did not differ from that using outlier-corrected data, even though the former included very high and unrealistic speeds on six flight-path segments (175, 381, 484, 611, 829, and 999 km/hr). These did not affect the average because they occurred over very short time periods between the first and last location points (32 sec to 7.2 min), and because we did not estimate groundspeed by averaging speeds of each flight-path segment. Investigators could increase the frequency of high-quality locations (LC > 0) by increasing PTT power, or, for large species, adopt new PTT models that incorporate global positioning systems (GPS; Microwave Telemetry, Inc. 2005). This would improve estimation of groundspeeds and airspeeds and their precision along individual flight-path segments.

Back-mounted PTTs may have reduced our estimates of pintail groundspeed; however, results from previous studies that addressed this issue have been inconclusive. For example, Butler et al. (1998) estimated a potential 5% increase in the energetic costs of flight of Barnacle Geese (*Branta leucopsis*) outfitted with 33-g PTTs. Because geese are able to reposition PTTs under their body feathers while preening (Butler et al. 1998), wind resistance due to PTTs may be reduced (Obrecht et al. 1988). Harnessed transmitters increased the energy cost of rapid flight in homing pigeons (Rock Pigeon, *Columba livia*; Gessaman and Nagy 1988), perhaps due to the vertically flattened posterior ends of the test transmitters (Obrecht et al. 1988). In wind tunnel experiments that tested the aerodynamic characteristics of three transmitter sizes attached to frozen Lesser Snow Geese and Mallards, streamlined transmitters created the least drag, and the smallest test transmitters (slightly larger than our 20-g unit [excluding harness]) created drag too small to be measured (Obrecht et al. 1988); the sloped anterior and posterior ends of our pintail PTTs mimicked the streamlined shape of these units. Pennycuick et al. (1996b) recently reduced their estimate of body-drag coefficients for flying birds from 0.4 to 0.08, suggesting that drag may not be as important as once thought. Based on this new information and our typical mean groundspeeds and airspeeds of PTT-tagged

pintails, we conclude that the variation in groundspeed caused by wind direction and speed likely overwhelmed wind resistance and mass effects of PTTs. Nonetheless, we encourage researchers to develop reliable, implantable PTTs for moderately sized waterfowl because of potential aerodynamic benefits and reduced energetic costs of flight.

ACKNOWLEDGMENTS

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